Zoomorphology (2003) 122:11–23
DOI 10.1007/s00435-002-0063-y

ORIGINAL ARTICLE

Andrea Cardini · Paolo Tongiorgi

Yellow-bellied marmots (*Marmota flaviventris*) 'in the shape space' (Rodentia, Sciuridae): sexual dimorphism, growth and allometry of the mandible

Received: 19 February 2002 / Accepted: 22 August 2002 / Published online: 18 October 2002

Abstract Geometric morphometrics was applied in a quantitative analysis of the morphology of the yellow-bellied marmot mandible. Five age classes were recognised by premolar toothwear, and the size and shape of the lower jaw were compared between sexes and among ages. Although the social role of adult males and females is markedly distinct, with the former mainly engaged to defend a territory with a female harem and the latter taking care of the young, mandible sexual dimorphism was moderate. On the contrary, form differences among age classes were conspicuous, and ontogenetic scaling, aimed at increasing mandible robustness, accounted for the majority of the shape change during growth. At least one mandibular shape modification, however, was related to the different behavioural ecology of immature and adult marmots. The mechanical efficiency of the superficial masseter and, thus, the strength of the incisor bite become so much greater in the sexually mature individuals that it cannot be interpreted as size-related adjustment. The need for stronger incisive bites is not explained by diet change, as the yellow-bellied marmot adults feed on the same grasses and forbs as the young and yearlings. Increasing the strength of the incisor bite is likely to be adaptive in order to provide adults with more efficient 'weapons' for intraspecific conflicts, and self- and kin-defence from predators. Morphological remodelling in the yellow-bellied marmot mandible seems to be more concerned with changes in size and behaviour during growth than with ethological differences between adults of the two sexes.

Keywords Marmot mandible · Geometric morphometrics · Allometry · Incisor bite

This paper is dedicated to F. James Rohlf on the occasion of his 65th birthday and in recognition of his important contributions to morphometrics

A. Cardini (✉)
via Porpora 125, 20131 Milan, Italy
e-mail: alcardini@interfree.it

A. Cardini
Dipartimento di Biologia Animale,
Università di Modena e Reggio Emilia, via Campi 13/D,
41100 Modena, Italy

P. Tongiorgi
Presidenza Facoltà di Agraria, via Kennedy 17,
42100 Reggio Emilia, Italy

Introduction

Yellow-bellied marmots (*Marmota flaviventris* Audubon and Bachman, 1841) are social ground-dwelling squirrels, widely distributed throughout the Rocky Mountains (Frase and Hoffmann 1980). Colonies comprise an adult territorial male with several females and their offspring, although single or paired animals are not uncommon. The diet is mainly composed of grasses, forbs and flowers, which are eaten selectively (Armitage 1979; Carey 1985; Frase and Armitage 1989).

Studies on their skull and jaw morphology are comparatively few, and often limited to providing cranial characters and measurements for taxonomic descriptions (Howell 1915; Frase and Hoffmann 1980; Hall 1981; Poole, unpublished observations). Only recently, Swiderski and Jansa (1999) analysed cranial and dental morphology of some Marmotini species to test the conservativeness and convergence of these traits during their evolution.

Ball and Roth (1995) found that neither body size nor diet seem to correlate with jaw muscle morphology of New World squirrels, while other factors (for example, cranial allometry in the pygmy squirrel, *Sciurillus pusillus* Desmarest, 1817) may have an influence on it. On the other hand, Thorington and Darrow (1996) found differences related to diet in the jaw muscles of Old World squirrels.

The morphology of the mandible (*os dentale*) in the Sciuridae has been extensively analysed by Velhagen and Roth (1997). However, their study focused mainly on New World tree squirrels; only one marmot species (*Marmota monax* Linnaeus, 1758) was included.

The present study investigates the functional morphology of the yellow-bellied marmot mandible, and its variation during growth and between sexes. The study was performed on the left hemimandible (to which we refer, henceforth, as 'mandible'), which was analysed by means of geometric morphometric techniques.

The analysis of the geometric form of the yellow-bellied marmot mandible aimed at answering the following questions:

1. What are the morphological changes, if any, that occur during the yellow-bellied marmot mandible growth?
2. Are males and females characterised by the same patterns of mandibular form change in spite of the different adult social roles?
3. May the geometric morphometric analysis give clues to identify important developmental (allometry and epigenetic action of masticatory muscles) or eco-ethological (diet changes and behaviour after sexual maturity) processes affecting the mandible morphology?

Materials and methods

Specimens

A sample of 75 specimens representative of the entire *M. flaviventris* range was used. Some of them were not included in the analyses of variance (ANOVA) as age or sex information was missing for seven specimens, and three specimens turned out to be outliers (see Results). Moreover, age class 0 was excluded from the ANOVA of the size and shape variables since it was represented by only three specimens.

All the specimens (see Appendix) belong to the National Museum of Natural History (Washington, USA) except one, which is part of the collection of the Natural History Museum (London, UK).

'Traditional morphometric' measurements and image acquisition

The distances between the paraconid and protoconid cusps of the lower left premolar were measured with a digital caliper to the nearest 0.1 mm. To test the precision of the caliper measurements, the paraconid–protoconid distance (PAPR) was taken seven times on a subsample of ten specimens (PAPR was measured by the same person over a period of 2 weeks in a row, with a 1-day interval between successive repetitions). The ANOVA for repeated measures indicated that there were no significant differences among the repetitions [$F(6,54)=1.046$, $P=0.406$].

A few distances between mandible regions related to incisor bite mechanics (see Results) were measured directly on the digital images using a computer graphics program (Corel Draw 1997). The measurement error was less than 1% when a 10-mm distance was repeatedly measured on the digital image of a millimetre graph paper ($n=15$, mean=10.10 mm, SD=0.100 mm). The distances measured on the two-dimensional images should approximate fairly well the three-dimensional, but relatively flat, hemimandible.

All images were captured on film using a reflex camera, with a 180-mm APO lens, locked to a copy stand. The mandible was laid on a horizontal plane whose inclination could be adjusted. A spirit-level was used to check that the lens and the specimen plane were parallel. The mandibles were set so that they always leaned the same way. To hold the scale of photographic reproduction constant, we chose to focus on the diastema region of the mandible, and kept the focal distance constant (1 m) by changing the height of the camera.

Digital images were scanned directly from the 35-mm negative film as greyscale images, at a resolution of 480 dpi with 210% magnification.

Geometric morphometrics

Landmark-based morphometric methods were chosen as they are more effective in capturing information about the shape of an organism and lead to powerful statistical procedures for testing differences in shape. Moreover, they provide researchers with accurate tools for visualising shape changes in a way that is both quantitatively correct and extremely suggestive (Rohlf and Marcus 1993). The two-dimensional approach implies a very limited loss of information for nearly flat objects, such as a marmot mandible (Velhagen and Roth 1997), and it allows depicting morphological changes using transformation grids (D'Arcy Thompson 1917; Bookstein 1991) which may give insightful clues for a thorough understanding of the shape variation.

As landmark-based morphometric techniques can be more easily explained, and understood, when illustrated with examples, the main steps of the analysis are described and further details are given while discussing the results.

1. Image acquisition (see above).
2. Choice and digitisation of homologous landmarks (see Smith 1990 for the definition of homology in morphometrics) used for 'capturing' the form (size + shape) of the mandible. Landmarks were digitised with the TpsDig 1.18 computer program (Rohlf 2001).
3. Superimposition of the specimens (Bookstein 1991, 1996). All the specimens need to be aligned in a meaningful way to avoid them being artefacts of the image acquisition and digitisation processes (Rohlf 1993). The generalised Procrustes analysis (GPA): (a) centres the set of landmark coordinates at their origin (centroid) and scales all the configurations to have unit centroid size (i.e. a measure of the overall size of the object computed as the square root of the sum of squared distances from the landmarks to the centroid of the landmarks), (b) finds the mean configuration (called the consensus) for the specimens in the sample and (c) rotates each configuration so as to minimise the total sum-of-squared residuals for the sample, and repeats the process (b) to (c) until it converges (TpsRelw 1.18 computer program; Rohlf 2001). To illustrate the GPA procedure, five marmot specimens (one for each age class) were chosen, and the results of the superimposition process are presented in Fig. 1.
4. Tangent space approximation of the shape space. After the GPA has been performed, each specimen corresponds to a point in the curved shape space (Slice 2001) and the metric that defines the shape space is the Procrustes distance (Bookstein 1991). In order to perform traditional statistical analyses on the matrix of shape coordinates, the specimens in the shape space must be projected to a tangent Euclidean space: the distance relationship between points is, thus, approximated as occurs in a flat map approximation of a small region of the earth's surface (Rohlf 1998). For the smallest shape variation around the point of tangency, the best point of tangency is the sample mean form.
5. Thin plate spline (TPS) and relative warps. The TPS is an interpolating function which proves useful to represent shape change as deformation among landmarks (Bookstein 1991). A "...way to think about this (TPS) is as if one form were printed on a transparent stiff plastic sheet and then manipulated by bending so that its 'shadow' takes on the prescribed landmark positions of the second form" (Zelditch et al. 1992). The TPS allows illustrating the overall shape change in the transformation from the consensus shape to that of a particular specimen. The shape change can also be partitioned into two components. The homogeneous transformations (stretching or compression)

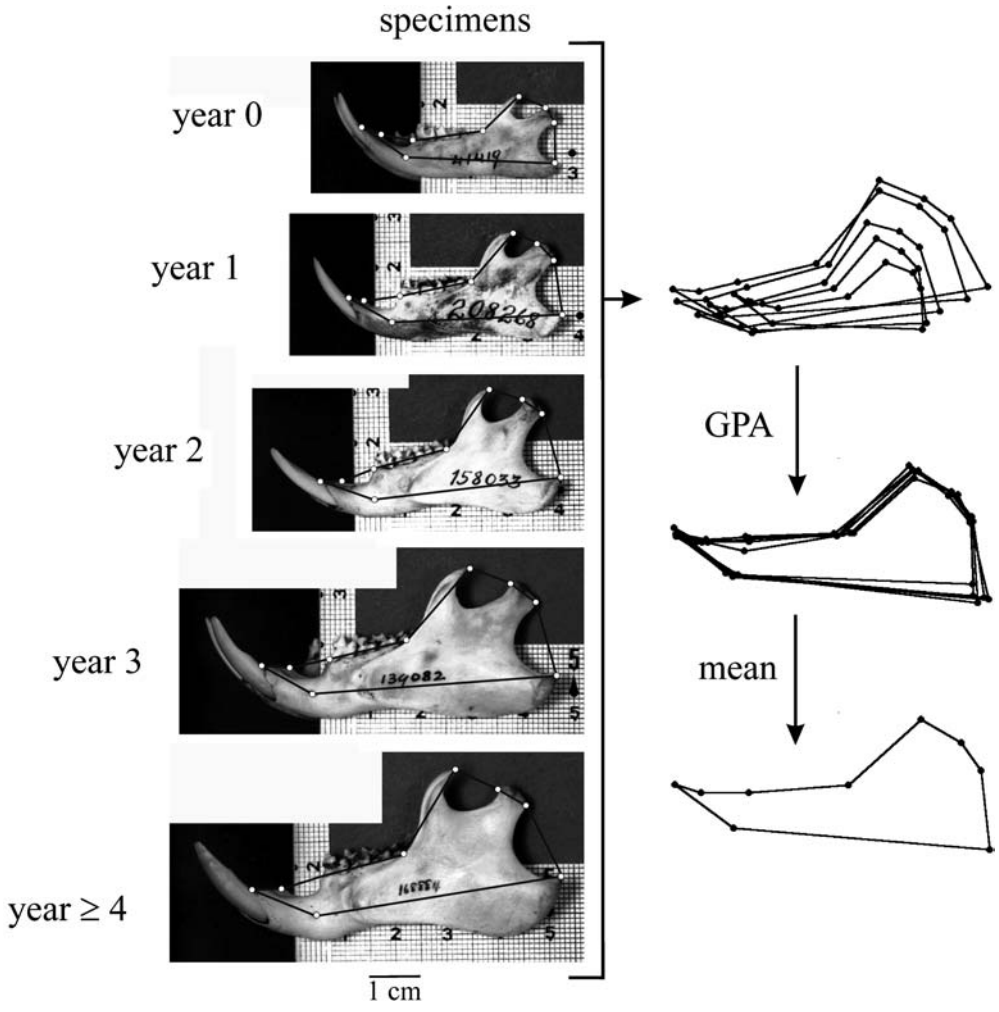

Fig. 1 Generalised Procrustes analysis (*GPA*): superimposition of five *Marmota flaviventris* mandibles, chosen as representative of the respective age class

are described by the uniform, or affine, component of shape change, i.e. those which leave all grid lines parallel as the same transformation occurs everywhere (Zelditch et al. 1992; Rohlf et al. 1996). All the non-homogeneous deformations, i.e. those occurring in a localised region of the object, are described by the partial warps, which are orthogonal shape variables ordered so that they represent differences from the largest down to the smallest scale (Rohlf et al. 1996). The mathematical derivation of shape variables in the TPS have been examined in several papers (Bookstein 1991; Zelditch et al. 1992; Rohlf 1993; Rohlf et al. 1996).

When large and small scale changes are weighted equally, a relative warp analysis is a principal components analysis of the covariance matrix of the partial warp scores (Rohlf 1993): as the TPS variables are orthogonal weighted linear combinations of the difference between each specimen and the (fixed) reference configuration, they can be analysed with the same statistical methods employed in traditional morphometrics (Rohlf 2000).

For simplicity, we will call 'shape variables' the whole set of uniform and non-uniform variables, while the more orthodox names (uniform component, partial warps and relative warps) will be used in all other cases.

6. Partial least squares (PLS) analysis (Rohlf and Corti 2000). It is a test for the covariation among two sets of variables (both of them shape variables, or shape variables and other variables such as traditional morphometrics ratios, ecological parameters, etc.). The PLS results in two sets of vectors (linear combinations), one for the partial warps (and uniform components, if included) and another one for the variables. The corresponding vectors of each set are paired (the first variable vector with the first shape vector, the second with the second, and so on). The vectors are not necessarily orthogonal within each set, and only the paired vectors are correlated (for example, the *i*th variable vector is independent of all shape vectors other than the *i*th; Rohlf 2001).
7. Test of form differences among groups (sex and age classes). Analysis of variance (using type III sum of squares) was performed on the following morphological variables: (a) centroid size, (b) uniform component, (c) a subset of relative warps, either excluding or (d) including the uniform component, and (e) some ratios between traditional morphometric measurements (see Results).
8. Regression of the shape variables on to the mandible size (centroid size or CS) and on to variables related to the masseter efficiency and power of the incisor bite (see Results).
9. Comparison of mean shapes for the age classes: the five consensus shapes (one for each age class) were plotted along the first two relative warp axes, and their differences illustrated by means of the TPS deformation grids.

The geometric morphometric analyses were performed using the computer programs of the TPS series, written by Rohlf (2001), GRF-ND (Slice 1993) and Morpheus (Slice 1999). For the statistical analyses SPSS 9.0.1 (1999), Statistica 4.5 (1993) and NTSYS-pc 2.1 (Rohlf 2000) were used.

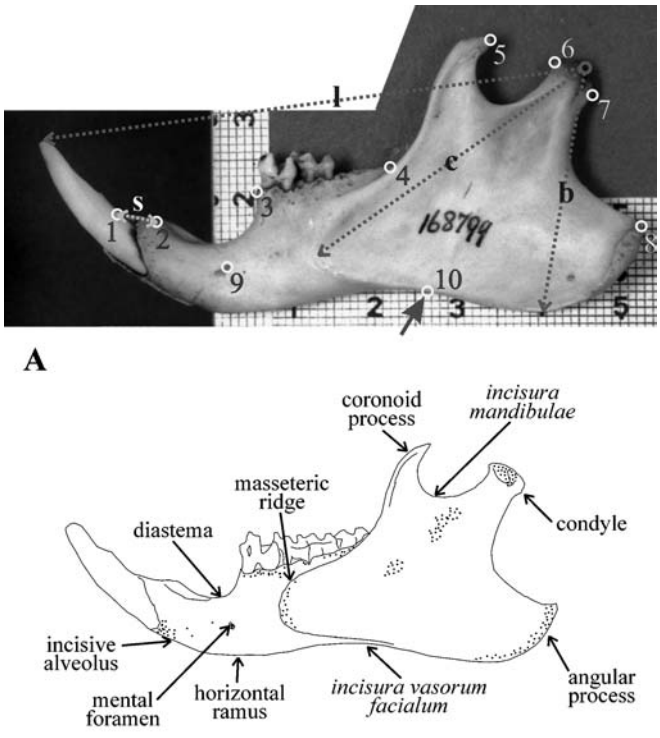

Fig. 2 **A** Homologous landmarks and distance measurements on the lateral side of the mandible. The *arrow* indicates the only landmark which cannot be reliably located. *l* Load arm in the incisor bite, *b* lever arm of the superficial masseter, *c* lever arm of the anterior deep masseter, *s* distance between landmark 1 and 2 (proportional to the length of the mandibular symphysis). **B** Anatomical regions of the mandible (labial side)

Landmarks

Ten homologous landmarks (L) were chosen on the lateral (labial) side of the left hemimandible (Fig. 2): (1) upper extreme anterior part of the incisor alveolus, (2) anterior top of the mandibular symphysis, (3) anterior extremity of the maxillary toothrow (premolar alveolus), (4) intersection of the dental ridge with the dorsal portion of the masseteric ridge (base of the coronoid process), (5) tip of the coronoid process, (6 and 7) anterior and posterior tip of the condyle, (8) posterior extremity of the angular process, (9) mental foramen and (10) *incisura vasorum facialum*.

Results

Landmark choice and precision, linear tangent space approximation to curved shape space and outliers

The medial (lingual) side morphology was not analysed as in only 12 specimens the two hemimandibles were separated and pictures of both sides could be taken. Moreover, among the landmarks that could be located on the mandible, 7 landmarks out of the 10 lateral ones and 13 medial ones are in common between the two sides (see list below), and almost all of them lie along the mandible outline. Due to the scarcity of internal landmarks, the morphological information captured on both sides of the mandible is very similar, as is easily revealed by a PLS analysis of the two sets of data (results not shown).

After having digitised the ten lateral landmarks seven times on a subsample of ten specimens, the precision of the digitising process was assessed for each landmark using profile plots of the *x*- and *y*-coordinates. The landmark (L10) located in the curvature of the *incisura vasorum facialum* showed evident discrepancies among the repetitions. This landmark was excluded from the analysis, which was, thus, performed using the landmarks L1 to L9.

The specimens were Procrustes superimposed, and the linear tangent space approximation to the shape space was tested by regressing, through the origin (consensus form), the distance in the tangent space on to the Procrustes distance (TpsSmall computer program, Rohlf 2001). No specimens were found to deviate appreciably from the linear regression line (r=1.00; slope, b=1.00).

One specimen (USNM 202937) turned out to be an outlier in the graphical analysis of the first four relative warps (uniform + non-uniform) either with or without including the juveniles (these four variates explained 71.8% and 69.4%, respectively, of the total variation in shape).

Marmota flaviventris age classes estimated by the premolar wear

The age classes of *M. flaviventris* were estimated by the lower left premolar wear (Van Vuren and Salsbury

Table 1 Premolar wear intervals and corresponding age classes. (*PAPR* Paraconid–protoconid distance)

PAPR intervals (mm)	Estimated age[a] (year)	Class[b]	Number
≤1.5	0	Juvenile	3
1.6–2.0	1	Yearling (age of dispersal)	7
2.1–2.5	2	Adults (age of first reproduction)	21
2.6–3.0	3	Adults	18
≥3.1	≥4	Adults (‘old marmots’)	23

[a] A four active months period corresponds to 1 year of age. Specimens with PAPR below 1.5 mm (lower limit for class 1) belong to age class 0; four specimens were not classified because of missing data for PAPR, but one of them was included in class 0 since its size was smaller than those of the two specimens classified as juveniles

[b] According to Armitage (1999)

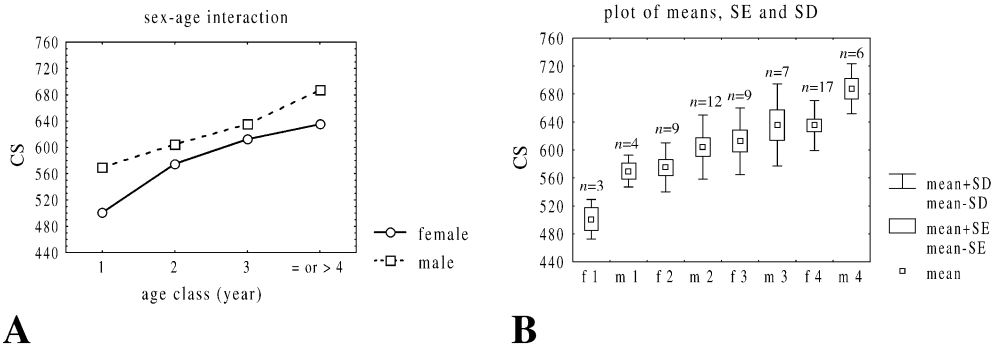

Fig. 3 **A** Absence of significant interaction between sex and age for the mandible size [centroid size (*CS*)]. **B** Plot of CS means, standard deviations (*SD*) and standard errors (*SE*) for sex and age 1–4 groups. (The CS, as well as the shape variables, have no units and their scores have only a relative value)

1992). The regression function y=1.52+0.12x, where y=distance (mm) between the paraconid and protoconid (PAPR) cusps of the lower left premolar, and x=months of activity (4 months/season) since the second active season (yearlings) to the fifth (4 years old), was used to find the wear intervals corresponding to five age classes (Table 1). Only three specimens with very small mandibles and the lowest values for PAPR (<1.5 mm) were classified as juveniles.

Since size increases as marmots grow older, at least until they reach sexual maturity, any 'age variable' should be correlated with the mandible size. The occurrence of such a correlation was tested for assessing the validity of premolar wear as an approximate estimate of marmot age in our sample. The linear regression of PAPR on to CS was highly significant [r^2=0.48; $F(1,69)$=64.08, P=5.5×10^{-12}], and the power curve PAPR=a×CS^b fitted the data even better [r^2=0.53; $F(1,69)$=79.203, P=2.1×10^{-14}]. The function y=a×x^b, or $\log_{10}y$=a′+b×$\log_{10}x$, is Huxley's formula for simple allometry (Huxley 1932; cited in Gould 1966 and Klingenberg 1996). When $\log_{10}$PAPR was regressed on to $\log_{10}$CS, the slope b of the regression line (b±95% confidence interval=1.58±0.35) was significantly larger than 1.00 (isometry).

Size and shape ANOVA and regression of 'shape' on to size

The juveniles (n=3) were excluded from the two-way (sex and age) analyses of variance of the mandible CS and shape variables, while the yearlings (n=7) were included regardless of their small sample size. The comparison between ANOVA results with or without yearlings showed that the small sample size of this class does not yield substantial changes in the F and Wilks' λ tests. As including yearlings was highly informative, they were used in all the ANOVA. In order to reduce the number of variables in the group comparison, shape analysis was restricted to the first four relative warps (which accounted for about 70% of the overall morphological variance).

The male mandible is larger than the female one (Table 2; Fig. 3). The CS differences among the age classes were highly significant, and there were no interactions between sex and age (i.e. the same trend, with males larger than females, was observed for all the age classes).

Table 2 Two-way ANOVA for centroid size (CS; sex×age 1–4)

Effect[a]	Sum of squares	*df*	*F*	*P*[b]
Sex	23,984.2	1	13.941	*0.000427*
Age classes (1–4)	31,983.2	3	18.591	*1.31E-08*
Sex×age	1,252.1	3	0.728	0.539
Error	1,720.4	59		

[a] The assumption of homogeneity of group variances was not violated [Levene's test: $F(7,59)$=0.666, P=0.699]
[b] Significant P in this and other tables are in italics

Following Rohlf et al. (1996), analyses of variances on the uniform and non-uniform components were first performed separately (Table 3). The ANOVA of the two components of shape change showed that the only significant differences were those among age groups. However, when uniform and non-uniform components were analysed together (Table 3), a slight (α=0.05) dimorphism in the mandible shape of males and females became evident.

The most visible features of the mandible morphological change during marmot growth are the uniform anteroposterior elongation and ventrodorsal narrowing in the juveniles and, to a smaller extent, in the yearlings (Fig. 4). This trend is reversed in the adults, whose mandible is relatively short (anteroposterior axis) and deep (ventrodorsal axis). Both in the uniform and non-uniform plots (Fig. 4) the backward displacement of the angular process in the older marmots is evident. The non-uniform shape change affects mainly the incisor alveolus and diastema region (L1, L2, L3), where the landmark density is higher. The backward displacement of L2 and the upward movement of L3 (the two landmarks delimiting the diastema) reveal an increase of the diastema concavity during growth. These shape changes are magnified in Fig. 5 to help their location, and they will be further discussed in the comparison of the traditional morphometric ratios with the geometric morphometric results. The relative position of the mean shapes of each

Table 3 Multivariate analysis of variance (sex×age 1–4) for the shape variables. The first four relative warps, with the uniform component excluded or included, represented, respectively, the 70.9% of non-uniform shape variation and the 69.5% of total shape variation

Variables	Effect	MANOVA				MANCOVA (CS covariate[d])			
		λ_{Wilks}	*F*	*df*	*P*	λ_{Wilks}	*F*	*df*	*P*
Uniform component[a]	Sex	0.902	3.000	2, 55	0.0580	0.973	0.752	2, 54	0.476
	Age (1–4)	0.561	6.152	6, 110	1.37×10^{-5}	0.783	2.347	6, 108	*0.0361*
	Sex×age	0.868	1.348	6, 110	0.242	0.839	1.653	6, 108	0.140
First four relative warps excluding uniform component[b]	Sex	0.880	1.807	4, 53	0.141	0.919	1.145	4, 52	0.346
	Age (1–4)	0.496	3.552	12, 140.5	1.27×10^{-4}	0.788	1.085	12, 137.9	0.377
	Sex×age	0.741	1.406	12, 140.5	0.170	0.736	1.414	12, 137.9	0.166
First four relative warps including uniform component[c]	Sex	0.820	2.912	4, 53	*0.0299*	0.911	1.271	4, 52	0.293
	Age (1–4)	0.404	4.778	12, 140.5	1.56×10^{-6}	0.696	1.687	12, 137.9	0.0769
	Sex×age	0.762	1.269	12, 140.5	0.243	0.749	1.327	12, 137.9	0.210

[a] The assumption of homogeneity of group covariance matrices was not violated [Box M test: M_{Box}=17.792; $F(21,1292.0)$=0.692, P=0.844]

[b] The assumption of homogeneity of group covariance matrices was not violated [Box M test: M_{Box}=57.3; $F(50,2533.8)$=0.867, P=0.734]

[c] The assumption of homogeneity of group covariance matrices was not violated [Box M test: M_{Box}=48.5; $F(50,2533.8)$=0.734, P=0.918]

[d] If $\log_{10}$CS is used as covariate instead of CS, there are very few changes in the P values of the statistical tests, and the analyses of variance results are equivalent (i.e. the factors with significant P are the same)

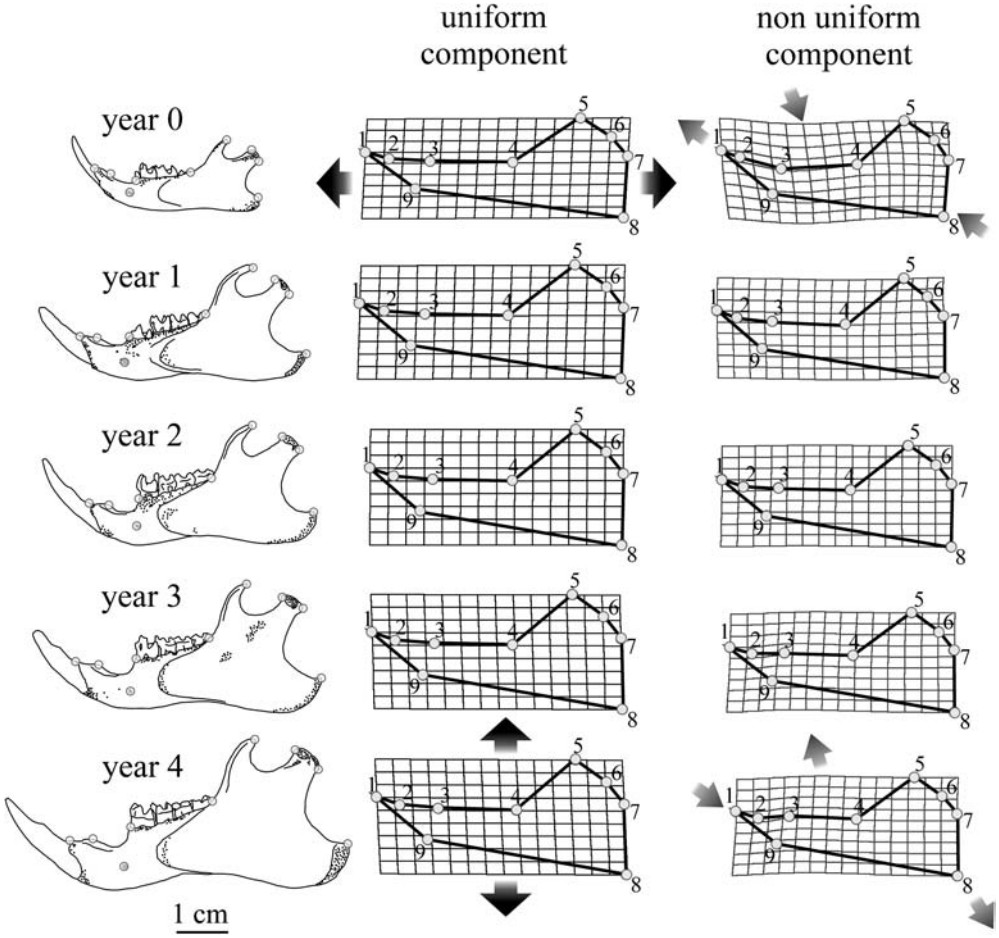

Fig. 4 Uniform and non-uniform component of shape change: transformation grids for the five mean forms of the mandibles of each age class (TpsRelw 1.18 computer program, by Rohlf 2001). The *arrows* help localise the directions of grid deformation for the youngest and oldest specimens

age group in the space of their first two relative warps (Fig. 5) clearly shows that, during yellow-bellied marmot growth, the changes in mandible morphology occur mainly in the first 2 years after birth, while there is little shape modification after sexual maturity is reached. However, it is worth observing that sexually mature marmots also go on increasing their size and changing their shape (Figs. 3, 5), even if at a progressively slower rate.

The centroid size was described by Bookstein (1991) as the only size measure that is uncorrelated with all

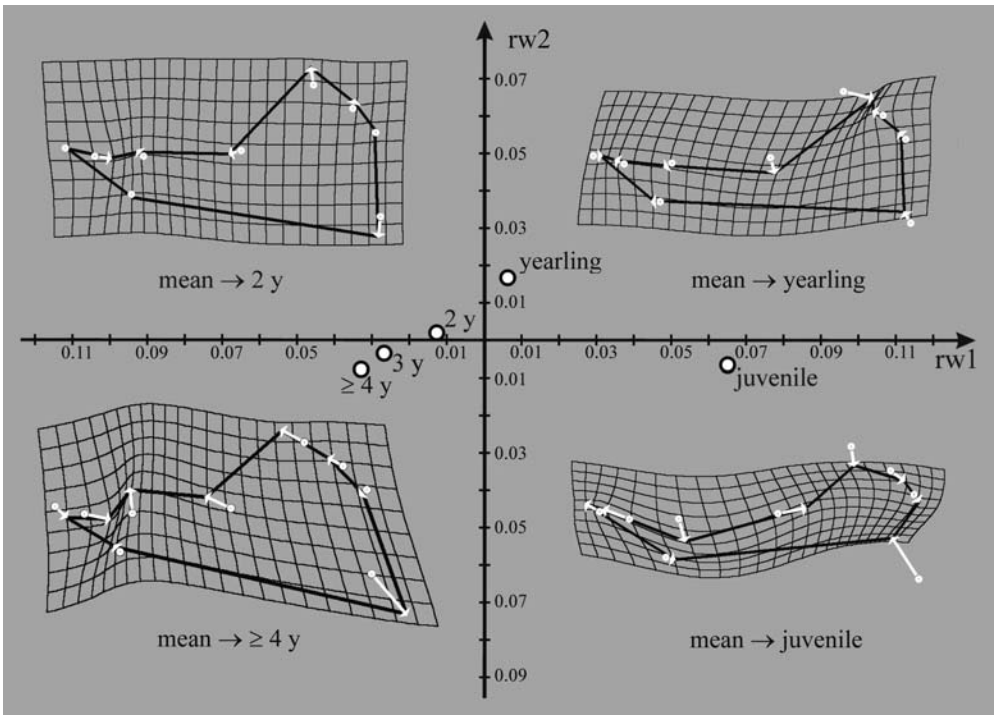

Fig. 5 Relative warp analysis (uniform component included) of the five mean forms of each age class. Ordination of the mean forms along the first two relative warp (*rw*) axes (97.7% of the total shape variation). The shape changes in the transformations from the consensus shape of all age classes (origin of the axes) to the mean shape of each class (*2 y*=2-year-old adult, etc.) are depicted either as transformation grids or as landmark displacement vectors (landmark position in the mean shape of all age classes → landmark position in the juvenile mean shape, etc.); the shape transformations were magnified to help localise prominent shape changes (juvenile deformation×3; yearling, 2 y ≥ 4 y deformations×6)

shape variables in the absence of allometry (differential growth). As a test for allometry a multivariate analysis of covariance (MANCOVA) with CS as the covariate was performed. After the size-related shape differences were removed, the yellow-bellied marmot mandible never showed significant sexual dimorphism, and also the age differences became negligible (Table 3). Only the uniform shape change (Table 3) remained significantly different (α=0.05) among the age classes.

As shape variables did not show a marked sexual dimorphism, and size differences between males and females of the same age were modest compared to differences among age classes (sex × age interaction not significant), the correlation between size and shape was tested on a common sample with both male and female specimens.

The first relative warp (uniform + non-uniform components; 39.9% of total shape variation) was used to test the best model for regressing shape on to size (Fig. 6). Log-transformed centroid size was used following Zelditch and Fink (1995) to take into account the progressive decrease of the rate of shape change during growth. Non-linear models led to r^2 values almost identical to that of the linear regression ($0.731 \le r^2 \le 0.752$). As none of the models fitted the data much better than the others, a multivariate linear regression of all the shape variables on to log-transformed CS was performed.

Before regressing the shape variables on to the size of the specimens of all the age classes, a test for common slopes was performed to decide whether separate slopes are needed (i.e. at least two groups differ in slope) or a common slope is sufficient for the entire sample (Rohlf

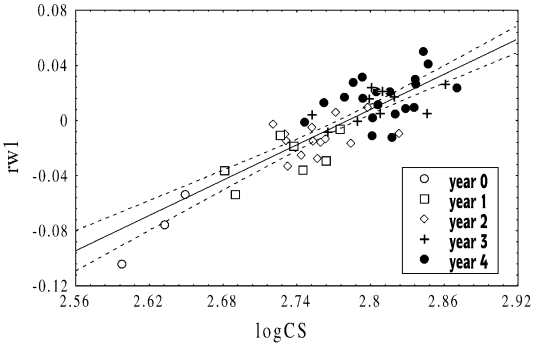

Fig. 6 Linear regression of the first relative warp (*rw*; all specimens included, 39.9% of the total shape variation) on to the centroid size (*CS*), with 95% confidence bands

2001). The three specimens of age class 0 were excluded from this test because of their very small sample size. As the result of the test for common slopes was not significant [Wilks' λ=0.512, $F(42,134.3)$=0.809, P=0.785], a multivariate test for homogeneity of the intercept values was performed to test for shape differences among groups with the covariate (size) held constant, as suggested by Rohlf (2001). The test was significant [Wilks' λ=0.315, $F(42,143.2)$=1.624, P=0.019] but not highly significant (P>0.01). Since regression slopes were similar in all age groups, and differences in intercepts were small, a multivariate linear regression of all the shape variables on to log-transformed CS, including all age classes (Table 4), was performed. As expected, the man-

Table 4 Linear regression of shape variables on to $\log_{10}$CS: multivariate tests of significance

λ_{Wilks}	Goodall's $F(14,57)$	P	Permutation test: $\lambda \leq$ observed[a]		Percent unexplained[a]	Generalised Goodall's $F(14,980)$	P	Permutation test: $F \leq$ observed[b]	
			Count	Percent				Count	Percent
0.149	23.31	1.5×10^{-18}	1	*0.1*	69.0	30.09	*<0.0001*	1	*0.1*

[a] It is the ratio between the sum of the squared Procrustes distances between each specimen and the reference (a measure of total variation in the sample) and the sum of the squared distances between each specimen Procrustes superimposed on its predicted configuration based on the regression analysis (a measure of the lack of fit; Rohlf 2001)

[b] One thousand random permutations; count and percent include the observed value

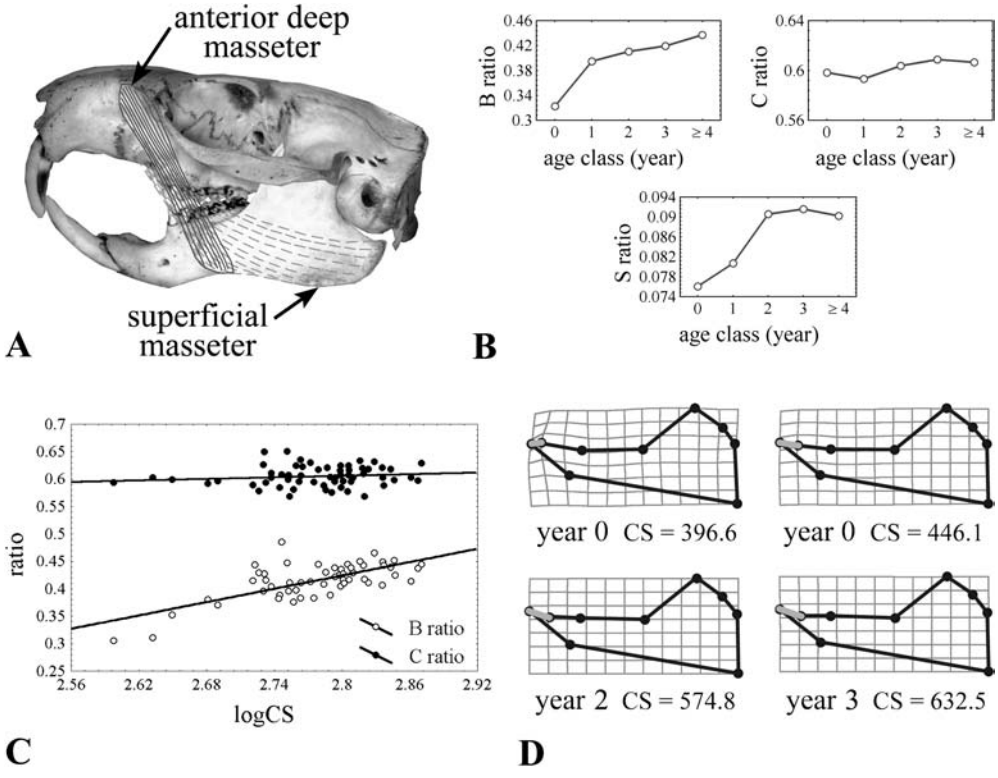

Fig. 7 **A** Superficial masseter and anterior deep masseter of *M. flaviventris*. **B** Plot of means for B (mechanical efficiency of the superficial masseter), C (mechanical efficiency of the anterior deep masseter) and S (relative length of the mandibular symphysis) ratios. **C** Linear regressions of B (superficial masseter efficiency) and C (anterior deep masseter efficiency) ratios onto $\log_{10}$CS. **D** First partial warp, for specimens of increasing size, showing the symphysis enlargement

dible shape was highly correlated to its size (P=1.5×10^{-18}) and also the percentage of shape variation explained by the size (31%) was highly significant (P<0.0001). The very low percentages of the permutation tests for the Wilks' λ and for the generalised Goodall's F (Goodall 1991, cited in Rohlf 2001) imply that the correlations between the shape and size are stronger than one would expect due to chance.

Mechanical efficiency of the superficial and anterior deep masseter, and power of the incisor bite

As the areas of insertion of the masticatory muscles in the posterior region of the mandible seem greatly affected by morphological remodelling during yellow-bellied marmot growth, possible variations in the mechanical efficiency of the masseter muscles (Fig. 7A) were analysed. Following Thorington and Darrow (1996), the distance from the mandibular condyle to the tip of the incisor was taken as the load arm for the incisor bite, and particular attention was paid to two other distances: (1) from the mandibular condyle to the most anteroventral point of the angular process (region of insertion for the superficial masseter) and (2) from the mandibular condyle to the anteriormost point of the masseteric ridge (region of insertion of the anterior deep masseter). These two ratios were indicated, respectively, as B=b/l and C=c/l ratios (Fig. 2A).

The B and C ratios were calculated for the *M. flaviventris* specimens (except the three outliers, and one which was devoid of the incisor), and for each ratio a two-way ANOVA test for sexual dimorphism and differences among age classes (1–4) was performed. Only the B ratio, which increases as the animals grow older, showed significant differences among age classes

(Table 5; Fig. 7B). Sex differences, and interaction between sex and age, were not significant. Furthermore, the B ratio was positively correlated with log-transformed centroid size [linear regression: r^2=0.468; $F(1,69)$=60.91, $P<10^{-10}$; Fig. 7C], but, in spite of the relation between the B ratio and size, the differences among age classes 1–4 remained significant (P=0.00289) even after removing the effect of size in a one-way ANCOVA with the centroid size as covariate. The homogeneity of C values was confirmed by the linear regression on to log-transformed centroid size: the regression line was almost horizontal [r^2=0.0201; $F(1,69)$=1.415, P>0.1; Fig. 7C] and even non-linear fitting always brought non-significant results.

The TPS deformation plots were examined to see how the change in the B ratio was depicted. As an increase of the B ratio is likely to affect mainly large scale features, it should be particularly evident in the uniform shape change. The transformation grids for the uniform component in Fig. 4 show a dorsoventral stretching and longitudinal compression of the mandible as marmots grow older. This transformation corresponds to an increase in mandible depth, and it is indeed the only shape feature still significantly different among the age classes after removing the effect of size (Table 3).

The development of a more compact and deep mandible during yellow-bellied marmot growth was captured either by the changes in the B ratio or by those in the uniform component, and turned out as the most evident morphological change occurring after birth. Nonetheless, by inspecting the non-uniform component (Fig. 4), two other apparently progressive modifications of mandible shape were found: the increasing concavity of the diastema and the enlargement of the mandibular symphysis. To test the latter observation, the interlandmark distance L1–L2 (symphysis) was measured, and the ratio L1-L2/load arm (called the S ratio) was computed to adjust for the differences in the incisor bite lever length. The S ratio did not differ significantly among age classes (1–4) and sexes in a two-way ANOVA (Table 5). The inspection of the S means plot for the five age classes (Fig. 7B) suggested to us that the major variation in the extension of the mandibular symphysis occurs during the first 2 years after birth, until sexual maturity is reached. Thus, the juveniles and yearlings (sexually immature) were gathered, and they were compared with the group formed by all the other age classes (sexually mature). The t-test was highly significant [$t(69)$=–2.74, P=0.0079], confirming that the enlargement of the mandibular symphysis and the sexual maturation happen in concomitance.

The relative increase in the distance between L1 and L2 is a very localised morphological change. As a matter of fact, it is clearly visible looking at the first partial warp deformation plot (Fig. 7D). The use of the partial warps one at a time may be erroneous, as demonstrated by Rohlf (1998), except, possibly, for the more local and more global ones (Rohlf 1999). The apparent agreement between the shape change depicted by the first partial warp and that described by the S ratio is supported by the highly significant multivariate regressions of the shape variables onto either B or S ratios (results non shown). Moreover, the PLS analysis of the covariation between shape variables, and B and S ratios, showed that the highest correlations of the first shape vector and the first variable vector (91.4% of the covariation, with a 4.50% probability of obtaining this percentage of covariation by chance in a 1,000 random permutation test) are those with the x- and y-axes of the first and sixth partial warps, and the uniform component ($r_{Pearson} \geq 0.56$). The shape changes visible in the uniform component and in the first partial warp have already been discussed, and the sixth partial warp showed an upwards movement of the premolar-molar toothrow as yellow-bellied marmots grow older. The deformations of the symphysis and toothrow, emphasised in the first and sixth partial warp plots, were visible also in the more reliable transformation grids of the uniform and non-uniform component as a whole (Fig. 5).

Table 5 ANOVA for B, C and S ratios (sex×age 1–4)

Effect	*df*	*F*	*P*
B ratio[a]			
Sex	1, 59	0.161	0.689
Age (1–4)[b]	3, 59	10.781	9.55×10^{-6}
Sex×age	3, 59	0.207	0.891
C ratio[c]			
Sex	1, 59	0.364	0.549
Age (1–4)	3, 59	1.443	0.239
Sex×age	3, 59	1.062	0.372
S ratio[d]			
Sex	1, 59	0.836	0.364
Age (1–4)	3, 59	1.832	0.151
Sex×age	3, 59	1.312	0.279

[a] The assumption of homogeneity of group variances was not violated [Levene's test: $F(7,59)$=0.467, P=0.854]
[b] In the unequal n HSD test, only the differences between age classes 1 and 4, and 2 and 4 were highly significant (P<0.001)
[c] The Levene's test was significant [$F(7,59)$=2.601, P=0.021], however, as the violation of the homoscedasticity assumption was not highly significant (P>0.01) and the variable was normally distributed, the ANOVA was performed
[d] The assumption of homogeneity of group variances was not violated [Levene's test: $F(7,59)$=1.134, P=0.354]

Discussion

Age classes and premolar wear

Voss et al. (1990) remarked that the variation in rates of dental attrition among contemporaneous individuals within populations as well as their variations over years are not known. Van Vuren and Salsbury's (1992) relation between age and premolar wear was calculated within a spatiotemporally homogenous sample (specimens col-

lected in the same area and year). This assumption does not hold for our heterogeneous sample. In spite of this, the highly significant correlation between premolar wear and mandible size suggests a close relationship between the rate of dental attrition and growth, and, in the absence of any other method to estimate the age of museum specimens, premolar wear seems to give an approximate but reasonable discrimination of the age classes. The positive allometry in the variation of PAPR relative to that of CS is explained by the premolar wear going on after the mandible growth has ceased.

Outliers

The sample turned out to be fairly homogeneous in spite of having several *M. flaviventris* subspecies and different age classes. The only exception to the strong intraspecific resemblance of yellow-bellied marmot mandibles was represented by the only available specimen of *M. flaviventris warreni* Howell, 1914 (USNM 202937). This subspecies was no longer included either in Frase and Hoffmann's (1980) nor in Hall's (1981) description of the yellow-bellied marmot. *Marmota flaviventris warreni* was, therefore, excluded from the analysis of the shape variables along with two other specimens (USNM 94343 and 42858), which were outside the 99% confidence ellipse in the linear regression of the first relative warp (uniform + non-uniform, all age classes included) on to the mandible size. The latter two cases could have been excluded just from the regression of shape on to size, but we preferred not to use them as they would produce unreliable results also in the multivariate analysis of covariance for the shape variables with size as covariate.

The three juvenile specimens were not considered outliers even if in the graphical analysis of the form (shape + size) variables they often were set apart from the cloud of points formed by all the other specimens. This result was likely to be due to the very small sample size of the age class 0. As having even a few juveniles in the study of the morphological variation of yellow-bellied marmot mandible was highly interesting (see also Discussion about masticatory mechanics), they were included, whenever possible, after checking that either with or without them the analyses produced similar results.

Size and shape variation

Yellow-bellied marmot mandible sexual dimorphism is negligible for shape but significant for size, with males larger than females at all ages, and the largest morphological changes occur in the 1st and 2nd years of life. These results are consistent with Poole's (unpublished observations) skull measurements on several *M. flaviventris* specimens of different ages. He found that the male skulls averaged larger than the female ones, and observed that the form changes in the skull were greater during the first 2 years after birth. The larger male size is likely to be related to the competition among males for territories inhabited by female harems (Armitage and Johns 1982; Armitage 1986, 1992). However, the different behavioural ecology of male and female yellow-bellied marmots, with the former more involved in the conquest and defence of a territory, seems to have led to a relatively small sexual dimorphism that does not concern shape. Loy et al. (1993) observed that sexual dimorphism in the cranium of Old World moles regards mainly size, and also in six species of the South American rodent *Proechymys* the morphological differences between sexes are limited to the size of their skulls (Corti et al. 2001). It is possible that when size differences between sexes are appreciable but modest, the size dimorphism may not be large enough to produce shape differences too. Nonetheless, Voss et al. (1990) warned that subtle sexual dimorphism may be difficult to detect in natural population samples, "where nothing is controlled and only coarse toothwear classifications are available to partition 'age' effects".

On the other hand, mandibular shape differences among age classes are certainly conspicuous. The most remarkable shape change during the yellow-bellied marmot mandible growth is the relative deepening and shortening of the adult mandible which produces a stronger and more efficient structure with increased surface for muscle insertion and reduced load arm length of biting and chewing. These results are consistent with Atchley et al.'s (1992) observation that muscle hypertrophy is a factor, heritable but epigenetic, which contributes to model the mandible shape in the rodents.

A simple developmental model for remodelling shape in concomitance with size increase is the differential growth rate of the mandibular regions, that may be achieved through changing the steepness of morphogen gradients (Lawrence 2001). Indeed, ontogenetic scaling (Gould 1966) accounts for a great deal of the variation in yellow-bellied marmot mandible shape. In other words, as individuals become larger (or older) their shape is remodelled by simply progressing further along a strongly allometric growth curve (Emerson and Bramble 1993). Most of the sexual dimorphic cranial traits in several primate species were traced to ontogenetic scaling (Shea 1983, 1985 cited in Emerson and Bramble 1993; Cochard 1985; O'Higgins et al. 2001). Voss et al. (1990) found that the first principal component calculated from craniodental measurements of the muroid rodent *Zygodontomys brevicauda* Allen and Chapman, 1893, was associated with the majority of the sample variance (>65%) and represented the effects of general growth (or size). The substantial shape change that accompanies size increase in the presence of strong allometry may serve to maintain functions that would be lost if growth proceeded geometrically, but it could also yield to functional change (Emerson and Bramble 1993).

Incisor bite mechanics and marmot behavioural ecology

Thorington and Darrow (1996) computed the ratios between the lever arm of a jaw muscle and the load arm to seek for morphological changes in the musculature, and associated skeletal elements, consistent with the diet of 11 genera of Old World squirrels. The superficial and anterior deep masseter, both involved in the power stroke of incisor biting and chewing, showed the greatest morphological variation (orientation of fibres, regions of insertions) among the squirrel jaw muscles. The highest ratios, and, thus, the greatest mechanical advantage, were found in those genera which feed on hard nuts (for example, *Ratufa bicolor* Sparrman, 1778, *Protoxerus stangeri* Waterhouse, 1842).

The analysis of the mechanical efficiency of the masseter muscles in producing the incisor bite confirmed that the dorsoventral stretching and longitudinal compression of the mandible visible in the deformation grids for the uniform component corresponds to a large increase in the superficial masseter lever/load arm ratio during yellow-bellied marmot growth. This change is not a simple size-dependent relation (Gould 1966), as it is highly significant even after removing the proportion of variation related to mandible size increase (B ratio ANCOVA). If the increased mechanical efficiency of superficial masseter is not only a size adjustment, could it imply a functional change in the adult incisor bite?

The lever arm in the power stroke of biting depends on the depth of the mandible, while in the power stroke of chewing, with the mandibular condyle unloaded, the length of the lever arm (the numerator in the B ratio) has no relevance (Thorington and Darrow 1996). Thus, the significant increase in the depth of the mandible (B ratio) during marmot growth indicates the need of more powerful incisor bites in older animals. Weijs et al. (1987) found that the morphological changes in craniomandibular shape of rabbits (*Oryctolagus cuniculus* Linnaeus, 1758) during growth resulted in adults with slightly larger maximum bite forces than juveniles, but over a more restricted range of gape. On the contrary, a wide gape angle and a relatively greater moment arm of the digastric muscle (involved in jaw opening) are effective in producing a more efficient jaw opening in juvenile rabbits. The remodelling of skull shape in growing rabbits emphasises those musculoskeletal features related to jaw-closing mechanisms (biting and chewing), and is likely to be an adaptation to different diet in newborn and adult animals: "the relative development and geometry of the mandible in neonatal mammals is biased in favour of the mechanics of jaw opening" (Herring 1985 cited in Emerson and Bramble 1993), which is generally similar to the mechanics of mammary gland suckling (Emerson and Bramble 1993). The gape angle in yellow-bellied marmots was not measured. However, the internally directed displacements of the angular (L8) and coronoid (L5) processes in the juvenile marmots produce a relative lengthening of the condylar process, and a concomitant narrowing of the posterior part of the mandible (Fig. 5). An elongated condyle and a thinner mandible may facilitate jaw opening, allowing a wider gape, that improves suckling efficiency in newborn marmots.

The mechanics of suckling during weaning has certainly an influence on the juvenile mandible morphology, and the rapid shift from a liquid (milk) to a solid (plants) diet after the first weeks of life may explain why mandibular shape changes are so pronounced in the juveniles. However, the superficial masseter mechanical efficiency (B ratio) and the symphysis robustness (S ratio) go on increasing at least until sexual maturity is reached, and the increase in the mechanical efficiency of the superficial masseter is 'more than proportional' to size increase and highly significant even if the juveniles are excluded (B ANCOVA with mandible size as covariate). As previously outlined, an increase in the superficial masseter lever arm/load arm ratio (B) strengthens the incisor bite. In the Old World tree squirrels (Thorington and Darrow 1996), the mechanical efficiency of the muscles involved in the incisor bites is correlated with diet preferences as the B ratio is larger in species feeding on hard nuts. In the yellow-bellied marmots the expansion of the symphysis and the overall increasing robustness of the mandible could be functionally related to the greater loads exerted on the adult incisors, but this is unlikely to be related to the diet. Carey (1985) found no differences in the proportion of plant types in faecal samples of juvenile, yearling and adult yellow-bellied marmots, and K.B. Armitage (personal communication) remarked that the young soon begin to eat the same plants as the adults, and the diet remains the same throughout life.

The marmots use their incisors not only for feeding but also as weapons in their conflicts against other marmots or predators. In a highly social species, where the adults take care of juvenile and yearlings, agonistic behaviour can be much more important after a marmot becomes sexually mature. Even if fights with predators may occur only occasionally, conflicts among marmots are more common: the males are engaged in territorial contests and the females may compete for social status or home range and need to protect their offspring not only against predation but also against infanticide by other marmots (Armitage and Johns 1982; Brody and Melcher 1985; Armitage 1986; Barash 1989). The winner of such fights will be more likely to transmit his genes to the next generation. A more robust mandible in the adult yellow-bellied marmots is thus part of development but it is also related to the advantage of having powerful weapons for settling conflicts.

Conclusions

The main conclusions are:

1. During the yellow-bellied marmot postnatal growth the mandible is largely remodelled. The major morphological changes occur before sexual maturity, in concomitance with the major size increase: the man-

dible becomes relatively shorter and deeper, and thus much more robust. Nevertheless, adult marmots go on growing, even if moderately, and slightly change their mandible shape following the same allometric trajectory as the young.

2. Sexual dimorphism is not very pronounced either for mandible size or shape, and the small differences between the shape of male and female specimens are a by-product of the moderate difference in their size (allometry). The slightly greater male size is related to sexual selection, with the male competing for territories with female harems.
3. Among the developmental processes that shape the yellow-bellied marmot mandible, ontogenetic scaling accounts for a rather large part of morphological novelties during postnatal growth. The enlargement of the area of insertion of the masseter muscles, the augmented power of the incisor bite and increased robustness of the adult lower jaw are the most prominent outcomes of growth. These changes cannot be simply due to diet shift, as, after weaning, young and adults feed on the same plants, but at least the relatively narrow and elongated juvenile mandible may be partially related to the mechanics of mammary gland suckling during the first weeks of life. On the other hand, although there are large differences in adult male and female social behaviour, agonistic interactions play an important role in the lives of both sexes. Adults use their bites as potent weapons for settling territorial disputes or for self and offspring defence against predators and conspecifics: males fight for territories, while females may be involved in contests for defending their young, the harem home range or their social status. The occurrence of such conflicts is relatively rare, compared to other marmot activities (Armitage et al. 1996), but their consequences on individual fitness may be huge. Therefore, we conclude that increasing mandible robustness and bites efficacy during yellow-bellied marmot growth might be mainly related to agonistic behaviour, while allometry and the epigenetic action of the muscles are among the most important processes shaping the marmot mandible.

Acknowledgments Several people contributed with precious advice or direct aid to this study. In particular, we wish to thank M. Corti, University of Roma 'La Sapienza', Italy, K.B. Armitage, University of Kansas, Lawrence, USA, R.S. Hoffmann and R.W. Thorington, National Museum of Natural History, Washington, USA, M. Ferraguti and G. Pacchetti, University of Milan, Italy, L. Sala, University of Modena and Reggio Emilia, F.J. Rohlf, State University of New York, USA, D. Van Vuren, University of California, Davis, USA, P. Jenkins and the mammal section team of the British Museum of Natural History (London), L. Gordon and all the other mammal curators of the National Museum of Natural History, Washington, USA, H. Seidler and K. Schaefer, University of Vienna, Austria, L. Spezia, Museo di Storia Naturale di Milano, Italy, and B. and F. Daverio. A special thank you to L.F. Marcus, American Museum of Natural History, New York, USA, for his incredible patience in reviewing this manuscript and his inestimable suggestions on statistics and morphometrics methods; his recent death left the 'morphometric community' orphan of one of its wonderful 'fathers'. This work was supported by grants from Italian Ministero dell'Università e della Ricerca Scientifica e Tecnologica (60% funds).

Appendix

Specimen catalogue numbers: USNM 99759 94343, 99760, 221898, 221896, 79365, 212471, 242645, 74373, 89312, 234960, 274340, 168884, 168883, 191366, 191367, 191369, 65920, 157828, 158033, 158980, 232665, 244551, 244552, 158500, 100532, 100533, 80360, 89311, 211232, 204891, 23951, 88243, 41419, 139082, 74057, 25523, 25524, 25527, 208268, 186520, 575170, 156923, 168477, 229842, 233382, 291192, 243663, 243664, 30143, 147183, 168799, 170148, 180918, 177297, 72565, 128750, 128753, 128754, 228271, 228273, 133505, 93688, 93689, 93708, 93690, 41914, 42368, 42112, 42080, 42858, 108792, 42122, 202937; BMNHL 40.823.

References

Armitage KB (1979) Food selectivity by yellow-bellied marmots. J Mammal 51:177–178

Armitage KB (1986) Marmot polygyny revisited: determinants of male and female reproductive strategies. In: Rubenstein DI, Wrangham RW (eds) Ecological aspects of social evolution. Princeton University Press, Princeton, pp 303–331

Armitage KB (1992) Social organization and fitness strategies of marmots. In: Bassano B, Durio P, Gallo Orsi U, Macchi E (eds) Proc 1st Int Symp Alpine Marmot and genus *Marmota*, Turin, pp 89–94

Armitage KB (1999) Evolution of sociality in marmots. J Mammal 80:1–10

Armitage KB, Johns DW (1982) Kinship, reproductive strategies and social dynamics of yellow-bellied marmots. Behav Ecol Sociobiol 11:55–63

Armitage KB, Salsbury CM, Barthelmess EM, Gray RC, Kovach A (1996) Population time budget for the yellow-bellied marmot. Ethol Ecol Evol 8:67–95

Atchley WR, Cowley DE, Vogl C, McLellan T (1992) Evolutionary divergence, shape change, and genetic correlation structure in the rodent mandible. Syst Biol 41:196–221

Ball SS, Roth VL (1995) Jaw muscle of New World squirrels. J Morphol 224:265–291

Barash DP (1989) Marmots. Social behavior and ecology. Stanford University Press, Palo Alto

Bookstein FL (1991) Morphometric tools for landmark data. Cambridge University Press, Cambridge

Bookstein FL (1996) Combining the tools of geometric morphometrics. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE (eds) Advances in morphometrics. Plenum Press, New York, pp 131–151

Brody AK, Melcher J (1985) Infanticide in yellow-bellied marmots. Anim Behav 33:673–674

Carey HV (1985) Nutritional ecology of yellow-bellied marmots in the White Mountains of California. Holarct Ecol 8:259–264

Cochard LR (1985) Ontogenetic allometry of the skull and dentition of the rhesus monkey (*Macaca mulatta*). In: Jungers WL (ed) Size and scaling in primate biology. Plenum Press, New York, pp 231–235

Corel Draw (1997) Corel Draw, version 8.0. Corel

Corti M, Aguilera M, Capanna E (2001) Size and shape changes in the skull accompanying speciation of South American spiny rats (Rodentia: *Proechimys* spp.). J Zool Lond 253:537–547

D'Arcy Thompson W (1917) On growth and form. Cambridge University, London Press
Emerson SB, Bramble DM (1993) Scaling, allometry and skull design. In: Hanken J, Hall BK (eds) The skull, vol 3. Functional and evolutionary mechanisms. University of Chicago Press, Chicago, pp 385–421
Frase BA, Armitage KB (1989) Yellow-bellied marmots are generalist herbivores. Ethol Ecol Evol 1:353–366
Frase BA, Hoffmann RS (1980) *Marmota flaviventris*. Mamm Species 135:1–8
Goodall C (1991) Procrustes methods in the statistical analysis of shape. J R Stat Soc B 53:285–339
Gould SJ (1966) Allometry and size in ontogeny and phylogeny. Biol Rev 41:587–640
Hall RE (1981) The mammals of North America, vol 1. Wiley and Sons, New York, pp 371–373
Herring SW (1985) The ontogeny of mammalian mastication. Am Zool 25:339–349
Howell AH (1915) Revision of the American marmots. North Am Fauna 37:1–80
Huxley JS (1932) Problems of relative growth. Methuen, London. Reprinted 1972, Dover Publications, New York
Klingenberg CP (1996) Multivariate allometry. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE (eds) Advances in morphometrics. Plenum Press, New York, pp 23–49
Lawrence PA (2001) Morphogens: how big is the big picture? Nature Cell Biol 3:E151–E154
Loy A, Corti M, Marcus LF (1993) Landmark data: size and shape analysis in systematics. A case study on Old World Talpidae (Mammalia, Insectivora). In: Marcus LF, Bello E, Garcia-Valdecasas A (eds) Contributions to morphometrics. Mus nac Cienc nat Madrid 8, Madrid, pp 215–240
O'Higgins P, Chadfield P, Jones N (2001) Facial growth and the ontogeny of morphological variation within and between the primates *Cebus apella* and *Cercocebus torquatus*. J Zool Lond 254:337–357
Rohlf FJ (1993) Relative warp analysis and an example of its application to mosquito wings. In: Marcus LF, Bello E, Garcia-Valdecasas A (eds) Contributions to morphometrics. Mus nac Cienc nat Madrid 8, Madrid, pp 131–159
Rohlf FJ (1998) On applications of geometric morphometrics to study of ontogeny and phylogeny. Syst Biol 47:147–158
Rohlf FJ (1999) Shape statistics: Procrustes superimpositions and tangent spaces. J Classification 16:197–223
Rohlf FJ (2000) NTSYSpc 2.1. Exeter Software, Setauket, New York
Rohlf FJ (2001) TPS series. Department of Ecology and Evolution, State University of New York, Stony Brook, New York. Http://life.bio.sunysb.edu/morph/
Rohlf FJ, Corti M (2000) Use of two-block partial least squares to study covariation in shape. Syst Biol 49:740–753
Rohlf FJ, Marcus LF (1993) A revolution in morphometrics. Trends Ecol Evol 8:129–132
Rohlf FJ, Loy A, Corti M (1996) Morphometric analysis of Old World Talpidae (Mammalia, Insectivora) using partial-warp scores. Syst Biol 45:344–362
Shea BT (1983) Size and diet in the evolution of African ape craniodental form. Folia Primatol 40:32–68
Shea BT (1985) Ontogenetic allometry and scaling: a discussion based on the growth and form of the skull in African apes. In: Jungers WL (ed) Size and scaling in primate biology. Plenum Press, New York, pp 175–205
Slice D (1993) GRF-ND generalized rotational fitting of n-dimensional landmark data. Department of Ecology and Evolution, State University of New York, Stony Brook, New York
Slice D (1999) Morpheus (beta version). Department of Ecology and Evolution, State University of New York, Stony Brook, New York
Slice D (2001) Landmark coordinates aligned by Procrustes analysis do not lie in Kendall's shape space. Syst Biol 50:141–149
Smith GR (1990) Homology in morphometrics and phylogenetics. In: Rohlf FJ, Bookstein FL (eds) Proceedings of the Michigan morphometrics workshop. University of Michigan Museum of Zoology special publication, Ann Arbor, pp 325–338
SPSS for Windows (1999) SPSS Inc. version 9.0.1. SPSS, Chicago
Statistica for Windows (1993) StatSoft Inc. version 4.5. StatSoft, Tulsa
Swiderski DL, Jansa SA (1999) Comparison of levels of homoplasy in morphology and cytochrome b sequences from marmotine squirrels. In: The joint meeting of the Society for the study of evolution, the American Society of Naturalists, the Society of Systematic Biologists, Abstracts
Thorington RW, Darrow K (1996) Jaw muscles of Old World squirrels. J Morphol 230:145–165
Van Vuren D, Salsbury CM (1992) The relation between premolar wear and age in yellow-bellied marmots, *Marmota flaviventris*. Can Field Nat 106:134–136
Velhagen WA, Roth VL (1997) Scaling the mandible in squirrels. J Morphol 232:107–132
Voss RS, Marcus LF, Escalante P (1990) Morphological evolution in muroid rodents. I. Conservative patterns of craniometric covariance and their ontogenetic basis in the neotropical genus *Zygodontomys*. Evolution 44:1568–1587
Weijs WA, Brugman P, Klok EM (1987) The growth of the skull and jaw muscles and its functional consequences in the New Zealand rabbit (*Oryctolagus cuniculus*). J Morphol 194:143–161
Zelditch ML, Fink WL (1995) Allometry and developmental integration of body growth in a piranha, *Pygocentrus nattereri* (Teleostei: Ostariophysi). J Morphol 223:341–355
Zelditch ML, Bookstein FL, Lundrigan BL (1992) Ontogeny of integrated skull growth in the cotton rat *Sigmodon fulviventer*. Evolution 46:1164–1180